Must all signals be evolved? A proposal for a new classification of communicative acts

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Abstract

While signals in evolutionary biology are usually defined as "acts or traits that have evolved because of their effect on others", work on gestures and vocalizations in various animal taxa have revealed population- or even individual-specific meanings of social signals. These results strongly suggest that communicative acts that are like signals with regard to both form and function (meaning) can also be acquired ontogenetically, and we discuss direct evidence for such plasticity in captive settings with rich opportunities for repeated social interactions with the same individuals. Therefore, in addition to evolved signals, we can recognise invented signals that are acquired during ontogeny (either through ontogenetic ritualization or social transmission). Thus, both gestures and vocalizations can be inventions or innate adaptations. We therefore propose to introduce innate versus invented signals as major distinct categories, with invented signals subdivided into dyad-specific and cultural signals. We suggest that elements of some signals may have mixed origins, and propose criteria to recognise acquired features of signals. We also suggest that invented signals may be most common in species with intentional communication, consistent with their ubiquity in humans, and that the ability to produce them was a necessary condition for the evolution of language.

Graphical/Visual Abstract and Caption

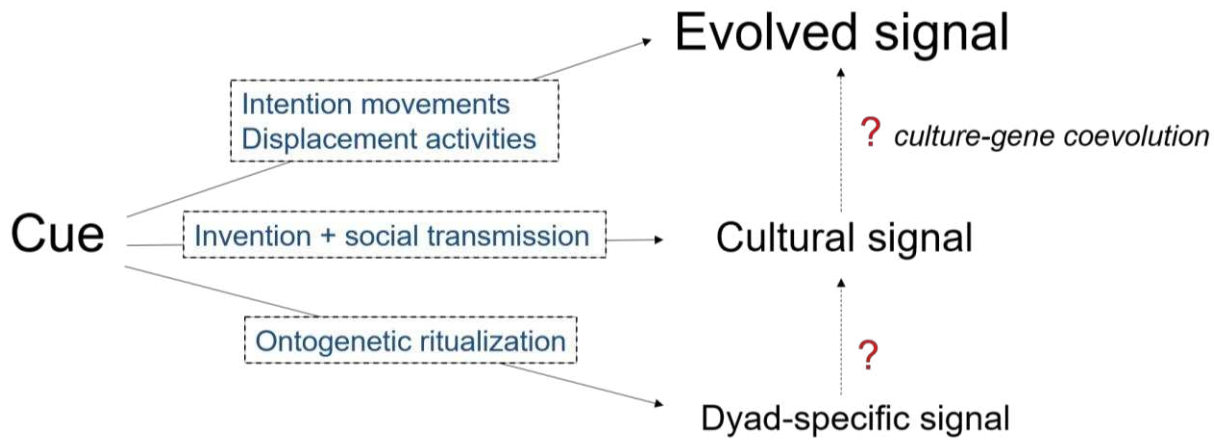

Figure 1 Onto- and phylogenetic origins of behavioural signals. Most behavioural signals are derived from cues that evolve into signals through intention movements or displacement acts. Through invention and subsequent social transmission, some cues or other invented behaviour patterns with communicative effect may become cultural, and may or may not subsequently become manifested in a species' innate repertoire (upper dotted path). Very few signals are derived from ontogenetic ritualization, which may or may not become group- and species-specific (dotted paths).

Introduction: Gestures as a special class of behavioural signals?

Communication mediates all social interactions between organisms, yet ambiguities and even disagreements exist about the most basic terminology (Maynard Smith & Harper, 2003; Ruxton & Schaefer, 2011). The term "signal" has not only been defined variously in the literature, researchers also disagree with regard to the role played in these definitions by the concepts of influence versus information (Krebs & Dawkins, 1984; Rendall, Owren, & Ryan, 2009; Scott-Phillips, 2008; Seyfarth et al., 2010). A problematic case in animal communication has become apparent in the highly interdisciplinary research area of great ape communication behaviour, which has for many years been dominated by disconnected studies of gesture, vocalization and facial expression (Slocombe, Waller, & Liebal, 2011; however, see e.g. Hostetter, Hopkins, & Cantero, 2001; Leavens & Hopkins, 2005 for integrated work on gestures and calls). In light of major discrepancies in the definition and operationalization of cognitive concepts, scholars increasingly recognise a need to integrate these

largely independent research traditions (e.g. Fröhlich, Sievers, Townsend, Gruber, & van Schaik, 2019b; Hobaiter, Byrne, & Zuberbühler, 2017; Liebal, Waller, Burrows, & Slocombe, 2013).

More than for other types of behavioural signals, learning mechanisms have been discussed for great ape gestures (Fröhlich & Hobaiter, 2018; Liebal, Schneider, & Errson-Lembeck, 2019; Pika & Fröhlich, 2019; Plooij, 1978; Tomasello, Call, Nagell, Olguin, & Carpenter, 1994). The most striking claim of why gestures are fundamentally distinct from other communicative acts was that they are acquired during an individual's lifetime during a process termed ontogenetic ritualization (OR) (Tomasello, 2008). While gestural researchers have begun to focus on ontogenetic plasticity and interactional experience (thereby emphasizing the underlying cognitive complexity) (Bard et al., 2014; Fröhlich, Müller, Zeiträg, Wittig, & Pika, 2017; Halina, Rossano, & Tomasello, 2013), they did not explore the implications of their conclusions for signalling theory. Meanwhile, examples of signal invention and transmission have also been reported for the vocal and facial domain as well as for behaviours often classified as stereotypical "displays" (Falótico & Ottoni, 2013; Perry et al., 2003; van Schaik, van Noordwijk, & Wich, 2006). Hence, an important question arises: Which features of a communicative act or structure – form, function and/or response – have to be evolved and innate properties for it to be classified as a signal?

We here argue that non-innate signals can only emerge in species capable of intentional communication. Intentionality, broadly defined as goal-directed acts or thoughts, is often cited as hallmark of human communication (Dennett, 1983; Grice, 1957). Because gestures are often used flexibly and intentionally, they have been contrasted with vocalizations, or any other innate signals (i.e. "displays") that are species-typical and often used non-intentionally (Corballis, 2017; Tomasello, 2008; Tomasello & Call, 2019). For instance, for a long time animal vocalizations and facial expressions were thought to merely reflect emotional arousal of the producer (Tomasello, 2008). With more studies adopting an inclusive and multimodal approach, distinguishing between gestures and vocalizations based on intentional use and acquisition processes has become problematic (Fröhlich et al., 2019b). Studies on chimpanzees' alarm and food calls, for example, have provided evidence that these calls are intentionally directed, given that they were socially used (e.g. directed at specific recipients) (Crockford, Wittig, Mundry, & Zuberbühler, 2012; Crockford, Wittig, & Zuberbühler, 2017) and associated with audience checking, gaze alternation and goal persistence (Schel, Townsend, Machanda, Zuberbühler, & Slocombe, 2013). Similarly, it has been shown that orang-utan facial expressions can meet some of the criteria for intentional production, as their "play faces" are modified depending on the recipient's visual orientation (Waller, Caeiro, & Davila-Ross,

2015). Therefore, all three signal types – gestures, vocalizations, facial expressions – can potentially be used intentionally.

Behavioural ecologists working on animal communication typically distinguish signals (i.e. structures or acts that evolved for their effect on receivers, see below) from cues (i.e. communicative by-products of behaviour). It could therefore be claimed that any communicative act that acquired its communicative function through an individual's lifetime, as has been suggested for gestures, cannot really be considered a signal. However, if these communicative acts serve similar functions as evolved signals, they should be classified as signals, and the signal category should therefore be extended beyond the innate, evolved origin.

Here, we will explore the aetiology of communicative acts, and ask about different origins and types of signals in an attempt to unify the terminology in animal communication research. It has been suggested that the most fundamental categories of communicatory acts are gestures versus facial expressions versus vocalizations etc., in part based on their aetiology (Arbib, Liebal, & Pika, 2008; Liebal et al., 2013; Slocombe et al., 2011). However, we will argue that this is suboptimal, because similar inventions have now also been found in vocalizations. We therefore suggest that a highly useful distinction would be between signals that are the product of evolution through natural selection (and thus species-specific), of invention and spread through social learning, i.e. cultural (and thus often population-specific), or of co-construction by two signallers after invention by one of them (and thus dyad- or individual-specific).

SIGNALS AS DEFINED IN EVOLUTIONARY BIOLOGY

In evolutionary biology, signals are thought to be the product of an evolutionary history. Specifically, a signal has been defined as "any act or structure which alters the behaviour of other organisms, which evolved because of that effect, and which is effective because the receiver's response has also evolved" (Maynard Smith & Harper, 2003, p. 3). Our focus here is on signals that have an exclusive or major behavioural component (acts), because static displays (e.g. sexual swellings, facial colouration, ornamentation) are unlikely to be any other than evolved. Admittedly, in most primate behaviour studies the signal interpretation usually remains based on plausibility, because the adaptive value of a communicative act is often inferred from an analysis of the social context. Thus, even if we can demonstrate how a signal fits into the sender's behavioural goals, this does not prove it is adaptive

(i.e. improves the sender's fitness relative to the absence of the signal). Worse, even if we can show that a behaviour is currently 'adaptive' in that it has overall positive fitness consequences, this still does not prove that it evolved for this particular function (Gould & Lewontin, 1979; Tinbergen, 1959). Nonetheless, it is widely accepted that signals evolved through natural selection and are adaptations.

Cues, on the other hand, have been defined as assessable animate or inanimate features of the world that are partly related to a condition of interest and thereby serve as a guide for future action (Bradbury & Vehrencamp, 1998; Hasson, 1994). In contrast to signals, these acts or traits did not evolve *because* of their effect on others. Importantly, many signals may have evolved from what once were cues (Laidre & Johnstone, 2013; Maynard Smith & Harper, 2003), or from incidental movements or responses of actors that happened to be informative to receivers (Krebs, Davies, & Parr, 1993). Many behavioural displays are thought to have evolved through *ritualization* (Huxley, 1914): exaggeration, repetition and standardisation (Tinbergen, 1952). Thus, ritualization is used to refer to the evolutionary modification of movements and structures that improve signal function. For instance, several primate species exhibit signals involving prominent postures or bodily movements that indicate an individual's travel motivation (e.g. Fischer & Zinner, 2011; Fröhlich, Wittig, & Pika, 2016; Gruber & Zuberbühler, 2013; McDonnell, 2003). These signals often constitute abbreviations of a species' natural movement, with individuals exhibiting a distinctive gait or positioning their body axis in the direction of travel. Such intention movements were ritualized over evolutionary time into highly stereotyped displays or signals (Daanje, 1951; Laidre & Johnstone, 2013; Tinbergen, 1952), conveying the sender's motivational state. With regard to facial displays, fear grins in primates are thought to largely resemble the reflex response with which to protect the sensitive parts of the face (i.e. eyes and mouth) from the attacker's impact (Krebs et al., 1993).

Animal vocalizations are among the most studied communicative acts in evolutionary biology, and there is little doubt that many of them are the product of natural selection: they are innate and species-typical with a tight link between form and function, although the proper context of application is often learnt (Bradbury & Vehrencamp, 1998). It has been argued that the human equivalents of animal vocalizations are non-verbal affective expressions, such as laughing and crying (Burling et al., 1993; Corballis, 2002; Ekman & Friesen, 1969; Scherer, Johnstone, & Klasmeyer, 2003). They may represent the leftover fragments of an originally much larger innate call system, which may have been critical for the transition between innate and learned vocalizations (Deacon, 1992). However, accumulating evidence shows that it is no longer warranted to draw a distinction

between “innate calls” and “flexible gestures”, as most vocal and gestural signals have a strong innate basis (Byrne et al., 2017; Price et al., 2015) and do not seem to differ substantially with regard to ontogenetic plasticity and intentional use (reviewed in Fröhlich et al., 2019b).

In sum, a signal is commonly defined by its function: it evolved for the purpose of conveying information to recipients, such that the information elicits a response in recipients, and the response results in fitness consequences that, on average, are positive for both the signaller and the recipient relative to the signal’s absence (Maynard Smith & Harper, 2003). Most behavioural signals evolved through ritualization.

DYAD-SPECIFIC, ONTOGENETICALLY RITUALIZED SIGNALS

Two additional mechanisms of acquisition different from the evolutionary account have been discussed, which are probably closely interlinked: ontogenetic ritualization and cultural learning. The hypothesis of ontogenetic ritualization (OR) originally proposed an alternative aetiology of gestures (Table 1) (reviewed in Byrne et al., 2017; Tomasello & Call, 2019). In the last two decades, a number of captive studies found indirect evidence that both form and function of great apes’ gestural “signals” are acquired entirely ontogenetically. In analogy to the ethological concept of signal evolution over phylogenetic time (‘ritualization’) (Plooij, 1978), OR proposes that gesture types are derived directly from repeated social interactions in which individuals participate through an individual learning process (Tomasello, 1990; Tomasello et al., 1994). In OR, an individual A first performs a physically effective behavioural sequence to achieve its goal of influencing individual B; over the course of repeated dyadic interactions, B learns to anticipate A’s likely forthcoming behavioural sequence on the basis of its initial step and responds ‘early’. Subsequently, A relies on B’s anticipation, producing only the initial movement to achieve its goal in a ritualized form: A’s behaviour has become a communicative signal (Tomasello & Call, 1997). Consequently, different dyads, even within the same social group, might use different gestures for the same purpose. This presence of many idiosyncratic and “one-way” gestures, and thus a lack of systematic group differences, would imply that a two-way learning process is involved. Although the current definition implies that signals must have acquired their function through natural selection, we suggest these OR acts fulfil the criteria for signals, and thus can be considered invented signals. There is no obvious alternative, because these acts are not cues, yet communicate (see Figure 1).

Table 1. Distinction of communicative acts according to origin

Type of signal	*label*	*Specific to*	*Examples*
evolved	**innate**	Species	Most ape gestures (Byrne et al., 2017), facial expressions (Vick, Waller, Parr, Pasqualini, & Bard, 2007) and vocalizations (Cheney & Seyfarth, 1990; Price et al., 2015)
		Species-context modified	Some alarm calls (Fichtel & Van Schaik, 2006)
invented	**cultural**	Group-population	Some gestures (Boesch, 1996; Hostetter et al., 2001; Kalan & Rainey, 2009; Moura, 2007; Nishida, 1980) Some non-vocal sounds, e.g. kiss-squeaks and whistles (Hardus, Lameira, Van Schaik, & Wich, 2009; van Schaik et al., 2003; Watts, 2016; Wich et al., 2012)
	dyad-specific	Dyad	Some gestures (Halina et al., 2013; Tomasello et al., 1994), capuchin conventions (Perry et al., 2003)

The theory underlying OR presumes that a gesture will be directed only at the individual with whom it was ritualized and will have the function of initiating the interaction from which it originated. Halina et al. (2013) proposed that evidence for ontogenetic ritualization would accumulate as more studies would show interactions that are both invariant within dyads (so that co-anticipation of actions can be achieved) and variable across dyads (so that different gestures are ritualized). We would thus expect that dyad-specific gestures may be quite common. However, it has been

highlighted that OR is a transmission process that affords low fidelity and is therefore unlikely to result in stable traditions spanning multiple generations (Boesch & Tomasello, 1998; Tomasello & Call, 1997). Indeed, details of these communicative acts are likely to change across generations, since an integral benefit (adaptive value) of this sort of "signal" lies in its malleability, which requires more focus on the signallers and provides more information about emotional engagement (see also Perry et al., 2003).

Therefore, while gesture researchers have contrasted "learned gestures" and "innate vocalizations" for a long time (Arbib et al., 2008; Armstrong & Wilcox, 2007; Corballis, 2002), they have not discussed this issue from an evolutionary perspective: do such learned behaviours qualify as signals? In recent years, accumulating evidence from the wild questioned the relevance of OR in great apes' natural communication, suggesting that the majority of the apes' gesture forms are in fact, like their vocalizations, genetically predisposed. Studies on great ape gestural communication in the wild by the "St Andrews Gesture Group" (Genty, Breuer, Hobaiter, & Byrne, 2009; Graham, Furuichi, & Byrne, 2016; Hobaiter & Byrne, 2011) yielded evidence for the existence of species-specific gestural repertoires in great apes (Byrne et al., 2017). Since OR assumes that gestures cannot be generalized across dyads, such an acquisition process would predict an enormous amount of effort for each individual to acquire a gestural repertoire that is understood by the majority of its group members – especially in fission-fusion, semi-solitary or less cohesive societies where group members meet only occasionally (Byrne et al., 2017; Pika & Fröhlich, 2019). In addition, the use of idiosyncratic and one-way gestures, and consequently the lack of shared meaning within communities should be more common than they seem to be. Hence, although OR remains an influential concept among the primate gesture community, critics argue that the literature on this mechanism of acquisition is problematic and contains theoretical and conceptual misunderstandings (Byrne et al., 2017; Hobaiter & Byrne, 2011; Pika & Fröhlich, 2019). However, innate gestures and those acquired through OR need not exclude each other.

Regardless of the outcome of this debate, the concept of OR, given its focus on the shortening of action sequences, is mainly applicable to gestures. The bulk of movements of the body and limbs, as well as body postures, are produced for non-social rather than communicative purposes (e.g. locomotion, ingestion, vigilance). Hence, contrary to other communication modes, observers always face the challenge to distinguish communicative acts (i.e. gestures/displays) from non-communicative actions – a fundamental assumption for OR. Vocalizations, on the other hand, are

thought to always have social function, which largely contributed to the common perception of them as evolved signals.

We think that some captivity effect might at least partly explain the divergent conclusions for the origins of ape gestures by different researchers (Bard et al., 2014; Perlman, Tanner, & King, 2012; Pika & Fröhlich, 2019). Although evidence for OR in gesture acquisition in great apes is often thought to be a consequence of the divergent research foci of individual research groups (Fröhlich & Hobaiter, 2018; Liebal et al., 2019), it is perhaps more significant that the evidence emanates from captive settings (Halina et al., 2013; Liebal, Pika, & Tomasello, 2006; Pika, Liebal, & Tomasello, 2003, 2005), with its vastly different social environments. In captive environments, individuals, especially those of fission-fusion species, are constantly surrounded by a large number of interaction partners and thus experience a higher frequency of repeated encounters of and interactions with the same individuals. OR may thus be fostered in captivity due to the very intense rates of interaction, and might reflect behavioural plasticity on top of available repertoires commonly observed in the wild. Even if this is the case, however, it does illustrate how rapid signalisation can arise.

Importantly, signals that develop through OR may be unique to the dyad (i.e. used by one individual and understood by another of the dyad), whereas invented signals can also be acquired by others through social learning and thus spread just like any other innovation. However, there may be enough affordances to make such dyad-specific signals rare compared to group- or population-specific signals, simply because most dyads will convergently arrive at very similar, perhaps even the same, signal. Perhaps, then, recognition of OR signals may depend on making descriptions sufficiently fine-grained.

There are therefore three possibilities of how the evidence regarding OR could be interpreted in comparative research. First, the mechanism of OR is indeed found, but specific to very few gestures (Tab. 1). Second, this co-construction process also applies to the emergence of other communicative acts in non-apes (Perry et al., 2003), but we have not systematically detected it yet. Thirdly, OR is an artefact of a specific sampling method, consequently leading to a number of misconceptions (Byrne et al., 2017; Pika & Fröhlich, 2019). Future work should attempt to distinguish between these three possibilities, which are not exclusive and may apply to different gestures.

INVENTED CULTURAL SIGNALS

Next to the evidence on OR, various studies suggest a third category of signals that has so far been ignored: those that are invented and then socially transmitted to group members (i.e. cultural signals, Tab. 1). For instance, the invention and socially induced imitation of novel sounds and vocalizations has been described in wild orang-utans, such as the "kiss-squeak" variants (a sound produced in distress, occasionally involving tool use), "nest smacks", "nest raspberries" (both produced during nest-building) and "throat scrapes" or "harmonic uuhs" (produced by mothers before retrieving their infant) (Hardus et al., 2009; Wich et al., 2012). In wild chimpanzees, sounds performed during grooming bouts ("e.g. "splutters" and "teeth chomps") seem to provide evidence for sound dialects (Watts, 2016). In captive settings, chimpanzees use several invented, attention-getting sounds or vocalizations (Hopkins, Taglialatela, & Leavens, 2007), which are transmitted from mother to offspring (Taglialatela, Reamer, Schapiro, & Hopkins, 2012). In the non-vocal domain, invented communicative behaviours have been described for two different species of capuchins: novel social conventions in white-faced capuchins (hand-sniffing", "sucking", "finger-in-mouth game") (Perry et al., 2003), and the "stone throwing display" exhibited by proceptive females of bearded capuchin monkeys to solicit copulations from males (Falótico & Ottoni, 2013; Visalberghi, Di Bernardi, Marino, Fragaszy, & Izar, 2017). In some habituated groups, wild capuchins have been observed to use stone-banging in aggressive displays that seem to deter predators (i.e. in inter-specific communication) (Moura, 2007). In addition, there are reports of conspicuous stone-throwing displays in four populations of West African chimpanzees, which likely serve a communicative function (Kühl et al., 2016). Hand-clapping in gorillas has been reported only sporadically in varying contexts in western gorillas, and it remains an open question to what extent the form and/or context-specific usage of this and other attention-getting behaviours is innate or culturally transmitted (Fay, 1989; Kalan & Rainey, 2009; Salmi & Muñoz, in review).

In sum, the evidence presented above seems to suggest that cues can be ritualized into signals over both phylogenetic (Maynard Smith & Harper, 2003) and ontogenetic time (Hopkins et al., 2007; Tomasello et al., 1997) (see Figure 1). Cues may become signals more easily when individuals start to use them in intentional ways. This suggests that one possible mechanism through which signal formation can proceed is developmental, which would be much faster than the regular evolutionary pathway. The loud scratch in chimpanzee and orang-utan mothers (Fröhlich, Lee, Mitra Setia, Schuppli, & van Schaik, 2019a; Fröhlich et al., 2016), for example, would be a potential signal that does not require any evolutionary changes in morphology, merely intentional use. Invented "signals" can then fulfil all the functions of innate signals in intelligent species.

The new environments we have created for great apes may also produce newly invented signals that spread through social learning. Captive settings, similar to periods of environmental stability and plenty, may provide opportunities for signal inventions and innovations, just like it fosters innovations in general (Lehner, Burkart, & van Schaik, 2010; van Schaik, 2016; but see Reader & Laland, 2003 for the view of necessity rather than opportunity being the mother of invention). Kummer and Goodall (Kummer & Goodall, 1985) argued that "within the limits, free time and energy thus seem to further innovation" (p. 205). However, necessity may also foster innovation (Reader & Laland, 2003): human-modified, artificial living spaces separating individuals from each other may also require the innovation or modification of signals that are not needed in the wild. For example, out of 68 motor and vocal 'signals' used in the social communication of a captive group of hamadryas baboons, nine were reported only in captivity (Kummer & Kurt, 1965). While we noted that cultural variants of calls in orang-utans have been reported in the wild, even more extensive and convincing evidence for invented ("species-atypical") signalling has been reported from captive settings, encompassing novel pant-hoot variants (Marshall, Wrangham, & Arcadi, 1999), pointing with hands and fingers (Leavens & Hopkins, 1998; Leavens, Russell, & Hopkins, 2010), "raspberries" and "extended grunts" in chimps (Hopkins et al., 2007), and "whistling" in orang-utans (Wich et al., 2009). Moreover, sifakas' innate alarm calls acquired a novel meaning in captive enclosures in comparison with those produced in wild environments (Fichtel & Van Schaik, 2006). In conclusion, captivity may have led to a proliferation of signal invention. However, cultural signals clearly are not limited to captive environments, perhaps unlike ontogenetically ritualized signals (however, see Plooij, 1978).

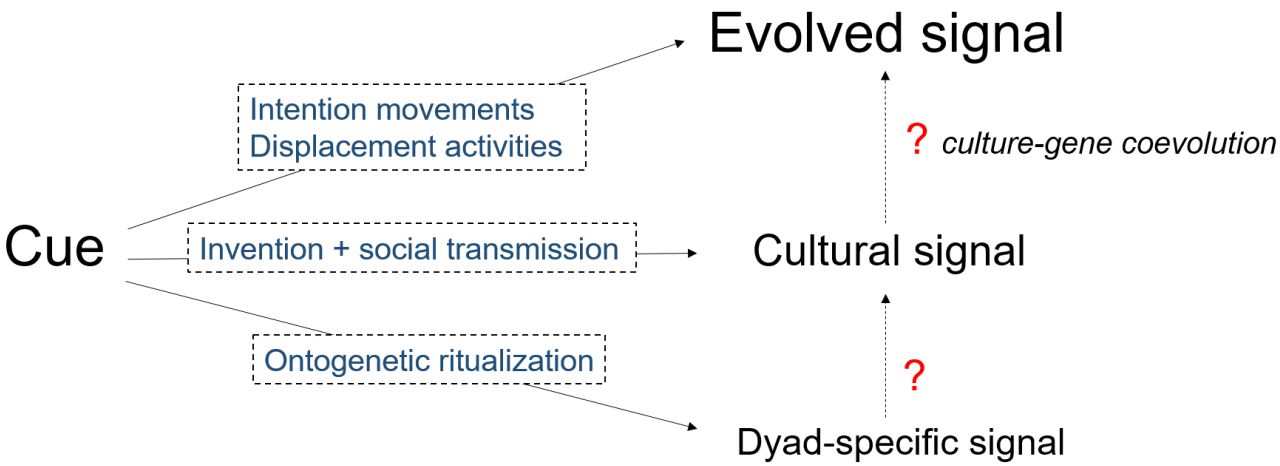

Figure 1 Onto- and phylogenetic origins of behavioural signals. Most behavioural signals are derived from cues that evolve into signals through intention movements or displacement acts. Through invention and subsequent social transmission, some cues or other invented behaviour patterns with communicative effect may become cultural, and may or may not subsequently become manifested in a species' innate repertoire. Very few signals are derived from ontogenetic ritualization (light grey path), which may or may not become group- and species-specific (dotted paths).

A NEW DISTINCTION: INNATE, CULTURAL AND DYAD-SPECIFIC SIGNALS

Based on this discussion, we propose to classify communicatory acts into *evolved* signals (species-specific) on the one hand and invented signals on the other, with the latter coming in two kinds: *cultural* (innovated and socially transmitted, and thus population- or group-specific) and *ontogenetically ritualized* (dyad-specific). Thus, the key criterion for this distinction is their ontogenetic origin (innate versus invented + socially transmitted or ontogenetically ritualized) (see Tab. 1).

As discussed above, it seems as if the production of most communicative traits is innate and species-typical, while the context of application, and thus comprehension, are partially learnt, or fine-tuned (Wegdell, Hammerschmidt, & Fischer, 2019). Early research on vocal development in vervet monkeys demonstrated that the acoustic structure of alarm calls resembles those of adults from an early age, whereas usage and comprehension of calls develop gradually, with observational learning involved (Seyfarth & Cheney, 1986; Seyfarth & Cheney, 1997). In human language, phonemes are

rapidly channelled through early experience (Kuhl, 2004; Ruben, 1997), resulting in an individually and culturally specific subset of sounds used for every day communication. It has also been shown repeatedly that a communicative act can acquire a *novel meaning* in different individuals and settings, irrespective of whether a signal's origin is evolutionary or ontogenetic (Tab. 1). An example of the first are the sifaka alarm calls mentioned above (Fichtel & Van Schaik, 2006). Examples of the second are provided by the leaf-clipping (a cultural signal: Whiten et al., 1999) exhibited in multiple populations of chimpanzees in roughly identical form, but apparently conveying different meanings at different sites (e.g. courtship and play) (Boesch, 1996; Nishida, 1980).

We acknowledge that our framework is not the first time a tripartite origin of signals has been suggested. In their study on gesture development in nursery-reared chimpanzees, Bard and colleagues (2014) proposed three different mechanism of acquiring gestures in young apes. In addition to genetic endowment (i.e. innate origin) and ontogenetic ritualization (i.e. social origin), co-construction "through inter-affective and inter-subjective processes based on shared communicative meaning" (p. 26) was put forward as a second invented origin of signals. Their account differs from ours in that it did not point to parallel cases in other species and non-captive contexts and did not examine the consequences for the signal concept in general..

PATHWAYS OF SIGNAL FORMATION

Are the three pathways to signal formation completely independent (see Figure 1)? The classic account of evolved signals assumes they derive from pre-existing intention or displacement movements. However, some observations suggest that some evolved signals might arise from cultural signals. Recent evidence from birds, cetaceans and primates showed that culture can affect selection pressures and population genetic structure, leading to a secondary form of evolution (reviewed in Whitehead, Laland, Rendell, Thorogood, & Whiten, 2019; Whiten, Ayala, Feldman, & Laland, 2017). It is entirely plausible to assume that this gene-culture coevolution also plays a role in the domain of communication (see Grant & Grant, 1996; Lachlan & Slater, 1999 for the case of bird song). Social conventions are dyadic social behaviours of a communicative nature and group-specific communicative acts (and thus cultural signals). Some noteworthy examples include unique grooming styles in Japanese macaques (Tanaka, 1998) and chimpanzees (McGrew, Marchant, Scott, & Tutin, 2001; McGrew & Tutin, 1978; Nakamura, McGrew, Marchant, & Nishida, 2000), including social scratching and hand-clasp grooming. Interestingly, a recent study reported on chimpanzees spontaneously copying a seemingly non-adaptive behaviour and potential signal ("grass-in-ear"),

suggesting a tendency in apes to copy an invention even when the behaviour has no obvious adaptive value (van Leeuwen, Cronin, & Haun, 2014). Robinson and Barron (2017) recently made a very similar suggestion when they argued that (non-communicative) instincts often evolved from learned responses in a process based on epigenetic changes that subsequently became genetically anchored.

We can ask for which communicative acts this pathway from cultural to evolved signals is most likely. Costly signals almost certainly evolved over a long time through the ritualization processes (i.e. repetition, exaggeration, standardisation). However, innovated "conventional" or "reputation" signals (Bradbury & Vehrencamp, 1998; Laidre & Johnstone, 2013; Maynard Smith & Harper, 2003) could have started out as cultural signals and become evolved signals with a genetic basis through gene-culture coevolution or genetic assimilation, also referred to as the Baldwin effect (Pinker & Bloom, 1990; van Schaik, 2016). These signals do not impose strategic costs on the signaller and are not physically linked to sender attributes, but still provide reliable information to receivers. Similar to the examples of signal invention discussed above, the encoding rules for conventional signals are thought to be arbitrary, and thus lack the direct link between signal and honest content seen in index and handicap situations (however, honesty can still be enforced by punishing deceitful individuals) (Bradbury & Vehrencamp, 1998). For example, the "grunts" and "girneys" commonly observed in rhesus macaques and chacma baboons are signals of benign intent that are relatively quiet and cost-free (Cheney & Seyfarth, 1997; Silk, Kaldor, & Boyd, 2000). Manual pointing, originally thought to be a gesture unique to humans (Butterworth & Grover, 1988), is frequently observed in captive groups of great apes to communicate with humans (Leavens, 2004; Leavens & Hopkins, 1998) and perhaps in some cases with conspecifics (Pelé, Dufour, Thierry, & Call, 2009; Savage-Rumbaugh, 1986). In contrast, pointing in natural environments seems to be very rare (but see Hobaiter, Leavens, & Byrne, 2014; Veà & Sabater-Pi, 1998). Hence, it has been suggested that pointing qualifies as innate signals for humans, but a socially learned one for great apes (Gómez, 2007).

Reputation signals additionally require that signallers and recipients have prior knowledge of one another's past signalling record, which occurs if individuals recognize one another, interact repeatedly, and remember the outcome of prior interactions (Laidre & Johnstone, 2013). These features must play a profound role in the emergence of novel "signals" in social groups. For primates, more than for any other order of animals, individuals remember the behaviour of other group members and modify their own behaviour accordingly (Tomasello & Call, 1997), which might

sometimes lead to consistent behavioural changes in the individual and subsequently in the population. Invention of novel signals in this group therefore seems entirely plausible

Finally, we cannot exclude that dyad-specific signals may be potential cultural signals in the making. Indeed, given the strong morphological and neurological constraints or affordances, OR may produce very similar signal form as the brief ritualization phase of cultural signals, and in fact may show overlap with innate signals. Thus, further study of the aetiology of these three kinds of signals may even help us understand the origins of new innate signals.

While OR and invention are not necessarily limited to captive settings, the latter can certainly foster their emergence by offering social settings with rich opportunities for repeated social interactions with the same individuals, as found for great apes and perhaps hamadryas baboons in captivity. These settings thus provide fertile opportunities for more detailed study of this process. After all, where communicative strategies are at least partly learned, innovation and learning errors can generate variation (Bradbury & Vehrencamp, 1998).

Moreover, we can observe *signal variants* in which the motor acts involved in the signal have changed (e.g. leaf-clipping produced with either hands, teeth or both in chimpanzees, kiss-squeak sounds modified by pressing lips on either hands or leaves in orang-utans; Tab 1.). Hence, there might always be intermediate cases, which may be examples of signal formation caught in the act. However, in principle, it is easy to distinguish between these three kinds of signals based on their distribution: species-wide, population-specific (or at least found in some populations and not in others), or dyad-specific (although it may arise in multiple dyads or populations due to shared contexts and affordances). Mixed cases may arise where novel elements are added to existing signals (for instance, when orang-utans start to make kiss-squeaks on leaves or twigs), and then the distribution of the elements can be used to parse the origin of the whole. Ideally, of course, such inferences are supported by more detailed ontogenetic studies.

An interesting task for the future is to examine the taxonomic distribution of the non-evolutionary pathway to signals. Their currently known distribution among primates suggests a strong bias towards great apes and capuchin monkeys. This may be due to biased research attention, given their reputation as prolific tool users. Widening the comparative approach might thus result in the detection of new invented behaviours. Alternatively, because intentional use should strongly

facilitate the process of signal invention, non-evolved signals may be most common in (or perhaps even limited to) species capable of intentional communication. Indeed, because humans also show all classes of signals recognized here, we currently consider this hypothesis more plausible.

NONVERBAL SIGNALLING IN HUMANS

Finally, when we look at the human condition, the evidence for all three categories of signals is overwhelming. In contrast to other animal species, we find invented signals in all forms and morphologies, including in facial expressions (which seems to be absent in primates) (Ekman, 1977). For example, emblems are gestures that qualify as cultural conventions. Unlike illustrators (co-speech gestures such as iconic and metaphorical gestures), these hand signals can stand on their own without speech and convey verbal meaning, such as the American OK sign (thumb and forefinger form a circle), the peace sign (two fingers up, palm facing outward), or approval sign (thumb up, hand in fist) (Johnson, Ekman, & Friesen, 1975). Facial emblems function like emblematic gestures for waving “hello” or “goodbye,” and like head nods for “yes” and “no.”, with their culture- or subculture-specific meaning (Ekman & Friesen, 2003). Language itself is a rich source of invented vocal signals (words), but conventionalized ritualized "vocal emblems" are also produced in a socially stereotyped way with characteristic intensity, such as the conventionalized vocal emblem "Ouch!" when experiencing pain (albeit interpreted as less spontaneous and reliable signals than “raw” affect sounds) (Johnstone & Scherer, 2000; Scherer, 1994). Work on creoles and emerging sign languages suggest that communicative acts that arose through OR could become cultural signals (Brentari & Coppola, 2013; Senghas, Kita, & Özyürek, 2004).

In the case of humans, differentiating between innate versus invented signals, while clear-cut in theory, may be just as difficult as for animals. All human infants are born with the same fundamental capacities for nonverbal (e.g. body postures, gaze) and verbal communication (e.g. phonemes). However, the way these social signals are applied in interpersonal relationships is learnt from parents, other caretakers and peers. Each nonverbal signal has its own meaning and is characterized by a specific developmental trajectory. For instance, the meaning of gaze with regard to type and duration is not genetically predisposed but acquired through social learning. While in some regions it is impolite to greet another person without seeking eye contact, the opposite holds for interactions in other regions. Every culture ascribes its own meanings and uses to social signals. To acquire the

diverse, culture-specific meaning in nonverbal and verbal communication, humans rely on long-term intensive social experiences in their early development.

Conclusion

We have proposed that a more effective distinction than the one between “gestures”, “displays”, “vocalizations” and “facial expressions” is one between innate signals that evolved through natural selection and invented signals that are learned during ontogeny. For many purposes, it will of course be useful to retain gestures, vocalizations and facial expressions as signal categories but there is no longer any reason to think of gestures as special relative to other signals because only they are subject to an underlying learning process (even if the concept of OR stands the test of time and turns out to be limited to gestures, not all gestures originated this way). It is also critical to consider that communicative acts can acquire novel meanings and that signal variants exist, irrespective of an evolutionary or ontogenetic origin.

The ubiquity of invented signals in humans supports the idea that species with intentional communication are more prone to invent new signals. Among primates, invented signals (particularly in the vocal domain) seem to be presentin great apes, capuchins and humans (but see e.g. Garland et al., 2011; Grant & Grant, 1996 for evidence of cultural signals in cetaceans and birds). Thus, language is strongly linked to such communicative creativity. Without this inclination to invent novel signals, modern language may never have emerged in the hominin lineage. Thus, given that great ape communication contains many examples of intentional use in both gestures and vocalizations (Cartmill & Byrne, 2010; Crockford et al., 2017; Leavens, Russell, & Hopkins, 2005; Schel et al., 2013), this ability may have served as a necessary (but obviously not sufficient) condition for the evolution of language in our ancestors.

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